

Interaction between *Papilio hectorides* (Papilionidae) and four host plants (Piperaceae, Rutaceae) in a southern Brazilian population.

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Abstract Larval development of *Papilio hectorides*, including time to pupation, pupal mass and mortality, was measured on four different plant species (two in Piperaceae and two in Rutaceae). The results were compared with oviposition observations carried out during the spring-summer period 1986 in one southern Brazilian population from a study site in Sapucaia, RS, Brazil. The rank order for plant suitability differed from the rank order of egg distribution in the field. The most heavily used plant in the field (*Zanthoxylum hiemale*) resulted in the highest growth rates in the laboratory, but a infrequently used species (*Piper amalago*) was equally suitable for larval growth. *Piper xylosteoides* produced a large proportion of males that had one extra molt; an extra molt also occurred at low frequency in *Zanthoxylum hiemale* and *Z. rhoifolium*.

Introduction

Comparisons of larval development on different host plants and egg distribution in the field have not always demonstrated concordance between rank order of female choice and plant suitability (see Singer, 1984 for a review). Larvae can feed on a wider range of plants than females actually use for oviposition (e.g., Wiklund, 1973; Berenbaum, 1978) and they can grow well even on introduced plants that have been incorporated into the diet (e.g. Scriber and Finké, 1978).

Larval development and survivorship in the field depend on a number of factors. The quality of the food source, determined by nutrient availability and presence of secondary compounds, affects the time needed by larvae for the completion of development as well as the mass achieved at the end of larval stage (see Scriber & Slansky, 1981 for a review). Because larvae are vulnerable to parasitoids and predators (Feeny *et al.*, 1985) and fecundity is related to female body mass in a number of species (e.g., *Papilio polyxenes*, Lederhouse, 1981; Lederhouse *et al.*, 1982), host

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plant utilization should evolve towards the production of the heaviest possible pupae in the shortest possible time. Therefore, both time to pupation and pupal mass are good measures of the suitability of a particular host species for its herbivores. Physical characteristics of the environment, such as solar radiation exposure (Grossmueller and Lederhouse, 1985), also influence larval growth. Consequently, larval developmental time, final mass and survival will depend on the ovipositing females' choice of the host plant and microhabitat.

According to this scenario, we expect selection to favor the utilization of the most suitable plants, balancing between developmental and survival optima. In order to investigate this question, we measured larval growth rates of *Papilio hectorides* Esper, 1794 on four host species found at a site in Sapucaia, RS Brazil. These measurements were used to ask whether rank order of suitability of these plants is related to the rank order in which females oviposit on them in the field.

In southern Brazil, *Papilio hectorides* is oligophagous on Piperaceae and Rutaceae (see Biezanko, 1959a, b; Biezanko *et al.*, 1974 for host plant records; eggs were also found on *Piper mikanianum* in Maquiné, RS and Moreira, Gramado, RS, pers. obs.). These butterflies lay small clusters of 1-8 round, orange eggs on the underside of the host plant leaves.

Methods and Materials

STUDY SITE AND HOST PLANTS

Field observations were conducted in a second growth area adjacent to Parque Zoológico de Sapucaia, Sapucaia do Sul, state of Rio Grande do Sul, Brazil (30°S, 51°W) in the spring-summer period, 1986. The area had been deforested and subsequently reforested with *Eucalyptus* trees. It was characterized by a patchy secondary native flora mixed with *Eucalyptus* trees. The potential native hosts present were *Zanthoxylum hiemale*, *Z. rhoifolium*, (Rutaceae); *Piper amalago*, *P. gaudichaudianum* and *P. xylosteoides* (Piperaceae). Introduced potential hosts were *Citrus limon* and *C. reticulata* (Rutaceae).

In order to evaluate the distribution of eggs in different host plants, we selected three 400 m transects that included a representative sample of sunny and shady, open and dense habitats. All species of Piperaceae and Rutaceae present in the transects were considered potential hosts, individual plants were counted and inspected for eggs. The eggs found were collected and transferred to the laboratory for measurements of larval growth rates. Each cluster was assigned to a single plant species. Plant species frequency in the transects was estimated by the percentage of individuals of a particular species relative to the others.

LABORATORY TESTS

In order to evaluate host plant suitability, we reared a total of 344 *P. hectorides* larvae on the four native plant species on which eggs or larvae were found in the field: *P. xylosteoides* (N=106), *P. amalago* (N=66), *Z. hiemale* (N=90) and *Z. rhoifolium* (N=82). Measurements of (1) time to pupation, (2) mass and (3) mortality in each instar and immature stages were taken. Larvae were placed in 100ml plastic containers and kept at 25°C under constant light conditions. Additional eggs for the trials were obtained from captive females, and these were

distributed equally among the four plants tested. Food was changed daily, from a store of leaves that was kept at 8°C for a period of up to one week. Larvae were weighed on a Bosch precision balance (accuracy: 1µg) within 24h of each molt and pupae were weighed three days after pupation.

In order to determine the leaf water content of each host tested, 10 leaves of each plant species were collected and weighed together fresh and again after seven days at 45°C in a convection oven. The loss in water due to storage was evaluated in a similar way, 10 leaves were weighed together fresh and again after a week in our 8°C storage chamber.

Results

HOST PLANTS AND OVIPOSITION RECORDS

Host plants of *Papilio hectorides* differed in growth form, leaf shape and texture, and frequency in the transects at the study site (Table 1). The *Piper* species differed greatly in frequency; *P. xylosteoides* and *P. gaudichaudianum* were particularly abundant both in sunny and shady sites. However, the nature of the leaves of *P. gaudichaudianum*, highly pilose and lignified, probably prevented its utilization by the ovipositing females. *Zanthoxylum rhoifolium* (Rutaceae) individuals sampled in the study area were almost always smaller than *Z. hiemale* and grew mainly in sunny sites along the transects, whereas *Z. hiemale* occurred in both sunny and shady conditions. The introduced *Citrus limon* and *C. reticulata* were rare in the study area; only one well developed individual of *C. limon* could be sampled in a shady site.

Except for *Z. rhoifolium*, leaf water content was similar among the plants and the small differences observed between the species were not likely to account for differences in nutrition efficiency (Table 1; see also Scriber, 1979b). In addition, the water loss during storage was small (*P.*

Table 1. Comparison between the native potential hosts *P. xylosteoides* (PX), *P. amalago* (PA), *P. gaudichaudianum* (PG), *Z. hiemale* (ZH), *Z. rhoifolium* (ZR) concerning growth form, leaf shape and texture, leaf water content (%), relative frequency (%), number of clusters, number of eggs and mean number of eggs per cluster.

Plant	Growth Form	Leaf Shape and Texture	Water Content (%)	Freq. (%)	N Clusters	N Eggs	eggs/Cluster
ZH	tree	compound, glabrous	76.8	4.5	15	90	6.0
PA	shrub	single, glabrous	70.0	3.9	1	6	—
PX	herb	single, glabrous	78.7	51.8	13	56	4.3
ZR	tree	compound, pilose	57.8	2.0	0	—	—
PG	shrub	single, pilose	—	37.8	0	—	—

xylosteoides: 4.38%; *P. amalago*: 1.43%; *Z. hiemale*: 2.74%; *Z. rhoifolium*: 3.42%) and these fluctuations probably did not influence the nutrition efficiency of the plants (Scriber, 1979b).

At the study site, eggs were found on three of seven potential hosts (see Table 1 for information on number of eggs found on each host). No eggs or larvae were observed on *Piper gaudichaudianum*. Larvae (N=3) were found on *Zanthoxylum rhoifolium*. One larva and one egg (sterile) were found on the introduced *Citrus limon*, but no utilization was observed for *C. reticulata* in the study site. In addition, most of the eggs were found in shady sites.

If we calculate a utilization index for each plant by dividing the number of egg clusters found on it by its frequency in the transects, the following rank order is obtained: *Z. hiemale* > *P. xylosteoides* > *P. amalago* > *Z. rhoifolium* (on which larvae were observed). The distribution of egg clusters in the field was different from the expected if the clusters were laid randomly on the four effectively used native plants according to the frequency that they were sampled (χ^2 test; $\chi^2 = 91.04$, $\chi^2_{4|0.001} = 18.467$). However, the data available is insufficient to ask if the differences were due to growth form or size of the plant. *Zanthoxylum hiemale* received more eggs than *P. xylosteoides* as a result of a difference in the number of eggs per cluster (Table 1) (t-test; $t=2.09$, $P=0.0233$). We had no evidence of missing eggs in the clusters collected in the field.

DEVELOPMENT AND GROWTH RATES

The quality of the host plant affected time to pupation; because larval stage is a vulnerable period, the plant species that resulted in the fastest development was considered the most suitable host (Table 2). Male and female growth was pooled because their larval development time did not differ significantly (Table 3). Time to pupation did not differ between *Z. hiemale* and *P. amalago*, but we found that (1) larvae grew significantly faster on *P. amalago* and *Z. hiemale* compared to *P. xylosteoides* and (2) on any of the three other species compared to *Z. rhoifolium*. Significant differences were also found when the congeneric pairs *P. xylosteoides* vs. *P. amalago* and *Z. hiemale* vs. *Z. rhoifolium* were compared (Table 4). Thus, the rank order for host suitability based on time to pupation was *Z. hiemale* = *P. amalago* > *P. xylosteoides* > *Z. rhoifolium*.

Final pupal mass differed among host plant species and was influenced by sex (Table 2). However, in the sample raised on *P. xylosteoides* larvae that experienced extra instars were heavier than the larvae that passed through the normal number of instars (see Instar Number section). Insects raised on *Z. hiemale* and *P. amalago* formed significantly heavier pupae than those raised on *P. xylosteoides* and *Z. rhoifolium*, females weighing more than males (Table 4, Table 5). We ranked the host plants based on mean pupal weight as: for males, *Z. hiemale* > *P. amalago* > *P. xylosteoides* > *Z. rhoifolium*; and for females, *Z. hiemale* > *P. amalago* > *Z. rhoifolium* > *P. xylosteoides*. However, significant differences between means were found in just four out of 12 comparisons (Table 4).

Table 2. Growth comparison of *P. hectorides* larvae raised on four host plants. t represents the the calculated value for the t-test (two-tailed; * significant at a 0.05 level); L, larvae; P, pupae; T, total. The abbreviations of the food plants are the same as in Table 1, PX5i and PX6i refer to individuals that went through five and six instars, respectively, among the larvae raised on *P. xylosteoides*.

plant	N	time to pupation (days)			t	pupal mass (mg)			mortality (%)			six instars occurrence			
		?	/			?	/	?	/	L	P	T	?	/	?
ZH	61	21.8	23.2	1.73	ns	22.4	746.8	835.9	13.1	15.2	27.1	1	0	1	1.6
PA	50	22.5	22.7	0.32	ns	22.6	721.0	763.2	11.9	11.9	22.4	0	0	0	—
PX	65	27.4	28.4	1.30	ns	27.8	698.1	681.5	27.4	18.5	41.6	15	4	19	29.2
PX5i	46	26.2	27.8	1.86	ns	27.0	673.6	650.3							
PX6i	19	29.2	31.5	1.15	*	29.7	744.2	853.3							
ZR	44	28.8	31.2	1.22	ns	29.8	640.5	703.1	24.4	15.3	35.9	1	0	1	2.3

Table 3. Comparison of time to pupation obtained on four host plants (one-factor ANOVA). Data on *P. xylosteoides* (PX) pool five instar larvae (5i) and six instar larvae (6i).

Source	DF	SS	MS	F
between plants	3	2159.944	719.981	51.344
within plants	216	3028.892	14.023	
total	219	5188.836		

Table 4. Tukey multiple comparison tests of the means of the time to pupation (Tp), and male and female pupal mass (Mp) on the four host plants. The abbreviations of the food plants are the same as in Table 1. Asterisks represent significance at 0.05 (*), 0.01 (**) and 0.001 (***) levels.

Comparison	Tp ? /	Mp ?	Mp /
PX vs. PA	10.442***	1.301	3.612
PX vs. ZH	11.441***	2.793	7.987***
PX vs. ZR	3.868*	3.050	0.791
PA vs. ZH	0.396	1.412	3.226
PA vs. ZR	13.163***	4.104*	2.476
ZH vs. ZR	14.122***	5.439***	6.061***

Table 5. Comparison of male and female pupal masses obtained on the four host plants tested (two-factor ANOVA). Data on *P. xylosteoides* (PX) pool five instar larvae (5i) and six instar larvae (6i).

Source	DF	SS	MS	F	P
host plant	3	478987.36	159962.46	14.70	0.0001
sex	1	101613.50	101613.50	9.35	0.0025
plant vs. sex	3	91702.29	30567.43	2.81	0.0403
error	212	2303115.89	10863.57		

Table 6. Comparison of development time and pupal mass between individuals that passed through five (5i) or six (6i) instars in the sample raised on *P. xylosteoides*. Comparisons between 5i and 6i larvae on time spent in the first two instars refer to the total number of larvae raised on this plant; for the comparison of the time to pupation all the pupae that eclosed were used (? and /); and for the comparison of the final mass, just males were used. Comparisons between larvae raised on *P. xylosteoides* and *Z. rhoifolium* refer to males only. Time is measured in days and mass in mg. t represents the the calculated value for the t-test (two-tailed); asterisks, the significance at 0.05 (*), 0.01(**) and 0.001(***) levels. The abbreviations of the food plants are the same as in Table 1.

comparison	5i	N	6i	N	t
PX vs. PX					
time spent in the 1st instar	3.9	58	4.5	21	2.67 *
time spent in the 2nd instar	4.2	58	5.0	21	2.60 *
time to pupation ? /	27.1	46	29.7	19	3.42 ***
mass ?	667.8	25	744.2	15	2.26 *
comparison	PX6i	N	ZR5i	N	t
PX vs. ZR					
time to pupation ? /	29.2	15	28.8	25	0.29
mass ?	744.2	15	640.5	25	3.69 ***

In the larval stage, *P. xylosteoides* and *Z. rhoifolium* caused twice the mortality observed on *P. amalago* and *Z. hiemale*; pupal mortality was similar on all host plants (Table 2).

P. hectorides diapauses in the pupal stage during the dry season. Most of our test insects did not diapause, eclosing 16-17 days of pupation (Table 7). Nevertheless, about 20% of the individuals in our experiment spent longer periods in the pupal stage (the longest was 158 days). We cannot determine the cause of the lengthening of the pupal stage because the larvae were kept under controlled temperature and light. However,

Table 7. Comparison of mean larval duration and median pupal duration (days) between the four plants. The abbreviations of the food plant are the same as in Table 1.

plant	larval instars						pupa
	1st	2nd	3rd	4th	5th	6th	
ZH	4.0	3.4	3.5	4.2	7.7	—	17
PA	3.3	3.1	3.8	4.5	8.0	—	17
PX 5i	3.9	4.2	4.5	5.7	9.2	—	17
PX 6i	4.5	5.0	4.2	4.2	4.8	7.7	17
ZR	4.1	3.5	4.5	5.9	12.0	—	16

Table 8. Comparison of mean larval mass one day after each molt (mg) between larvae on the four plants. Mean egg weight equals 1.3 mg (N= 266). The abbreviations of the food plant are the same as in Table 1.

plant	instars					
	2nd	3rd	4th	5th	6th	
ZH	8.7	34.4	116.1	477.8	—	
PA	9.1	37.0	129.9	554.9	—	
PX 5i	7.5	27.5	106.1	511.2	—	
PX 6i	5.9	21.3	64.4	214.7	716.6	
ZR	9.2	31.2	115.0	436.3	—	

this diapause was not correlated with host plant species, sex, number of instars in the larval period or relatedness of offspring from captive females.

A mean of the time spent in each instar and larval mass after each molt is presented in Tables 7 and 8.

INSTAR NUMBER

Although the majority of the larvae passed through five instars, some individuals passed through an extra molt. The proportion of six-instar larvae differed among food plants and sexes (Table 2); *P. xylosteoides* was the plant which had the highest proportion of six-instar individuals and the occurrence of one extra instar was more common among males.

The occurrence of one extra instar increased the time to pupation of the individuals that fed on *P. xylosteoides*; the increase in final mass placed six-instar individuals raised on this plant species near to that on *P. amalago* and *Z. hiemale*. Since first and second instars were significantly

longer in six-instar larvae than in five-instar ones (Table 6), total time to pupation was also extended (Table 6). This elongation in the larval stage may explain why males with an extra instar were significantly heavier than five instar-ones (Table 6), leading to a significant interaction between food and sex in the comparison of mean pupal weight (Table 5).

In attempt to sort out the effects of the number of molts and time to pupation on the final mass, we compared six-instar males raised on *P. xylosteoides* with five-instar males raised on *Z. rhoifolium*. The duration of the larval stage, that time when larvae can feed, was similar between the two groups; mass acquisition, however, differed (Table 6). In this particular case, the time that larvae had the opportunity to feed was not the limiting factor in terms of mass acquisition. However, it was not possible to separate the effects of the number of molts from the difference in food quality, since the two groups under comparison fed on different plant species.

Discussion

Growth rate, pupal mass, fecundity and larval survival all seem to positively correlate with efficiency of host use (Wiklund, 1973; Courtney, 1981; Lederhouse *et al.*, 1982). Therefore, it is expected that natural selection will favor insects that oviposit on potential hosts in the rank order of their suitability (Singer, 1971; Jaenike, 1978; Rausher, 1985). However, there are examples of field observations which fail to show this expected ranking (Chew, 1977; Courtney, 1981, 1982).

In the population investigated, the rank orders for plant suitability and number of eggs found differed. Larvae developed equally well on a heavily used host (*Z. hiemale*) and on a plant that received few eggs (*P. amalago*). The abundant *P. xylosteoides*, the third-ranked host in terms of larval development, was also heavily used.

Most of the eggs were found on two unrelated plants that differed in growth form, leaf shape and abundance and a preference for shady sites was observed. Since *Z. hiemale* and *P. amalago* were similarly abundant and distributed both in sunny and shady sites, the difference in utilization between these two plant species cannot be attributed to unequal probability of encounter. Their distinct growth form, leaf size and shape, and, probably, secondary chemicals (see Feeny *et al.*, 1983; Baldwin and Schultz, 1988) are stronger discrimination cues for the ovipositing females and may cause differences in acceptance. *P. xylosteoides*, especially abundant in shady sites, was the second ranked host in terms of number of eggs found. The difference in number of clusters between *P. xylosteoides* and *Z. hiemale* was not as pronounced as the difference in absolute number of eggs received, which resulted from a significant difference in the average number of eggs per cluster. The cause(s) of the difference in mean cluster size between these two host species remains to be investigated, but it is possibly a response to intrinsic qualities of each of the plants (see Pilson and Rausher, 1989 for a comparison).

Zanthoxylum rhoifolium was mostly distributed in sunny sites, which may have an influence on its low utilization, assuming the females to have a preference for shady sites.

The estimates of growth rate demonstrated that unrelated plants can be equally suitable for larval development of *P. hectorides*. *Zanthoxylum hiemale* and *P. amalago* resulted in the fastest development, heaviest pupae and lowest mortality among the four plants tested. Contrasts between congeneric pairs showed remarkable differences in suitability. The differences in the leaf water content and texture may have some influence in the differential performance observed between the species of *Zanthoxylum*, but the same explanation is not valid for the two *Piper* species.

In those plants that supported less efficient growth, *P. xylosteoides* and *Z. rhoifolium*, the time needed by a larva for the completion of its development was longer and the final mass was smaller than the equivalent values obtained for *Z. hiemale* and *P. amalago*. Thus, in general, additional time in the larval stage could not counterbalance the poorer quality of the two low ranking hosts in terms of larval development. However, the occurrence of an extra instar, with a consequent increase on the time that larvae spent feeding, increased the final mass of the individuals raised on *P. xylosteoides* to a value comparable to the ones obtained for the most suitable hosts, *Z. hiemale* and *P. amalago*.

The occurrence of extra molts was related to host plant species and butterfly sex. Larvae raised on *P. xylosteoides* that underwent an extra instar (about 30% of the total) showed a significant increase in mass. The physiological event of passing through an extra instar seems to be acting in conjunction with the elongation of the larval period, increasing the pupal mass as a result. Interestingly, almost all the six-instar individuals obtained in this experiment were males. Because the extra molt tends to increase the final mass, and also because body mass is related to fecundity (Lederhouse *et al.*, 1982), we would expect females to be more frequent among individuals that passed through six instars. Scriber (1979a) reported the occurrence of extra molts in larvae that experienced a poor diet, but he did not include individual records on sex, time to pupation, or pupal mass.

The observations reported here suggest that diet breadth in the population studied is constrained by females oviposition behavior; the larvae can perform well on a plant that has been underexploited by females in the field. However, growth rate estimates were done under controlled conditions in the laboratory, preventing us from evaluating other ecological factors that can play an important role in larval success and survival in the field (*e.g.*, differential predation of eggs or larvae according to their location or host, Dempster, 1984; Grossmueller and Lederhouse, 1985). The observed micro habitat preferences for oviposition, the non-utilization of a potentially suitable plant and the observed differences in the number of eggs per cluster between the two most

heavily used plants in the field are points that demand deeper investigation.

Acknowledgements. Our thanks go to Phil DeVries, Larry Gilbert, Janet Lanza, Bob Lederhouse, Mike Singer and Bob Srygley and for valuable criticism and suggestions that very much improved the manuscript. Thanks also to Keith Brown Jr. for criticism on C.M.P. Master Thesis. CNPq fellowship to C.M.P. made this research possible.

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